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Sound producing system of a pempherid fish

Sound Characteristics and the Sound Producing System in

Silver Sweeper, *Pempheris schwenkii*

(Perciformes, Pempheridae)

M. Takayama*, A. Onuki[†], T. Yosino[‡], M. Yoshimoto[§], H. Ito[¶], J.

Kohbara** and H. Somiya^{††}

*, **Faculty of Bioresources, Mie University, 1515 Kamihama, Tsu, Mie
514-8507, Japan. [†], ^{††}Graduate School of Bioagricultural Sciences, Nagoya
University, Chikusa, Nagoya 464-8601, Japan. [‡]College of Science,
University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan.

[§], [¶]Department of Anatomy, Nippon Medical School, Bunkyo-ku, Tokyo
113-8602, Japan.

^{††}Corresponding author: H. Somiya, E-mail: somiya@agr.nagoya-u.ac.jp

The sound characteristics and the sound producing system in silver sweeper, *Pempheris schwenkii*, are described. The main frequency component of the emitted sounds was 100–300 Hz, the mean duration of the sounds being 56 msec. The sounds were produced by paired extrinsic sonic muscles vibrating the swimbladder. The sonic muscles originated on the pterotic bones and extended to the anterodorsal surface of the swimbladder, and were innervated by two branches of the occipital nerves. Moreover significant sexual dimorphism of the sonic muscles was observed, those in males being three times as large as in females.

INTRODUCTION

Neurobiological details concerning peripheral and central sound producing systems in sonic fishes have been steadily accumulating in recent years, although such studies have usually involved Siluriform (Ladich & Bass, 1998), Batrachoidiform (Fine, 1997), Beryciform (Carlson & Bass, 2000) and Scorpaeniform fishes (Yoshimoto et al., 1999). Understanding the neurobiology of the peripheral and central sonic systems of Perciform fishes, is however still fragmentary.

The silver sweeper, *Pempheris schwenkii* Bleeker (Perciformes: Pempheridae), is a common species inhabiting reefs and coral heads in the

tropical Indian and Western Pacific Oceans. In Japan, it occurs from the temperate coastal waters of Chiba Prefecture to the subtropical waters of the Ryukyu Islands. Sweepers are strictly nocturnal, possessing large eyes and extremely compressed bodies. They aggregate in caves or under overhangs by day and emerge at night to feed on zooplankton around the reef (Gladfelter, 1979). Uchida (1933) included a brief mention of the ability of the species to produce sound, in his study of the life history of *Pempheris japonica* Döderlein.

So far as can be ascertained, no investigations dealing with the physical characteristics of fish sounds and/or the sound producing organs, have included the Pempheridae (Tavolga, 1971; Fine, 1997; Ladich & Bass, 1998; Carlson & Bass, 2000). The main objective of this study, therefore, was to analyze the spectral properties of the sounds produced by silver sweeper and to describe the sound producing system, including its innervation pattern.

MATERIALS AND METHODS

Three live specimens of *Pempheris schwenkii* (86.4–106.0 mm SL) were made available for sound analyses in September 1998 by 'Shima Marineland aquarium' (Shima, Mie, Japan). The sounds emitted by silver sweepers held by hand in the air were recorded with the plaintalk microphone

(unidirectional electret microphone, sensitivity: $-9.5 \text{ dBV} \pm 5 \text{ dBV}$ at 1.0 kHz relative 1.0 V/Pa) of a personal computer (Macintosh). The microphone was placed within 5 cm of the fish. Sounds were digitized at 44.1 kHz and downsampled to 11 kHz. The signals were analyzed using the program SoundEdit Pro (Macromedia, Inc.). Sonograms were calculated using fast Fourier transform (FFT). Thirty additional specimens (70.0–134.7 mm SL) were collected in June 1997 and 2000 by hand or gill net off Cape Maeda (Onna village, Okinawa, Japan) for anatomical observations. The fish were deeply anesthetized with tricaine methanesulfonate and then fixed in 10% formalin.

Anatomical observations on the swimbladder and its associated structures were made under a dissection microscope. The right and left sonic muscles were removed and weighed separately. To standardize for variations in specimen size, the sonic muscle-somatic index (SMSI) was calculated as total sonic muscle mass/total body mass $\times 100$, following Connaughton et al. (1997). Bony structures were observed in cleared preparations stained with alizarin red S and alcian blue.

To trace sonic muscle innervation patterns, osmic acid was used. General terminology of the nerves was followed Parenti & Song (1996), although the term 'occipital nerve' was used rather than 'spino-occipital nerve' because the

nerve emerging through the foramen on the occipital region of the cranium. The first spinal nerve was defined as that emerging from the first free vertebra, and the second as that emerging from the second vertebra (Parenti & Song, 1996).

RESULTS

In distress situations, sounds were emitted by the fish in both water and air. Although sound production was observed in both males and females, only male sounds were recorded in this study, typical recordings lasting for about fifteen seconds. Silver sweeper produced only a single sound type in air, representative sonograms of three separate sound emissions and their correspondent osillograms being shown in Figure 1A. The duration of the three sounds was 75, 60, and 75 msec, respectively. At the beginning of the sound recording experiments, 24 sound emissions were recorded within a 15 second period. At first, the fish vocalized strongly, with sounds of longer duration (75–70 ms), but within about 1–2 minutes, the vocalizations rapidly diminished. By the end of each recording period, the duration of single sounds had decreased to about 20 msec. In a typical recording, the mean duration of sounds emitted was about 56 msec (mean \pm S.D. = 56.4 ± 12.5 , $N = 24$). Each sound consisted of several pulses, the number ranging from 2 to

7 (mean \pm S.D. = 4.9 ± 1.1 , N = 24). A representative sonogram and oscillogram of a sound emission comprising 7 pulses is shown in Figure 1B. The frequency distribution of that sound is shown in Figure 1C, the main component being rather low, covering the 100–300 Hz wave band. They showed three harmonically-related peaks, a possible fundamental peak at 100 Hz and two harmonics at 200 Hz and 300 Hz, respectively (Figure 1C).

The sound producing structures in silver sweeper included three components: a pair of cylindrical sonic muscles (Figures 2), a single swimbladder with two chambers serving as resonators (Figure 2), and the occipital nerve, which innervates the sonic muscle (Figure 3).

The cylindrical sonic muscle originates on the bony wing of the pterotic bone, passes under the ventral process of the posttemporal bone, and reaches across and over the dorsal side of Baudelot's ligament (Figure 2B) to terminate on the dorsal face of the anterior chamber of the swimbladder adjacent to its counterpart from the other side (Figure 2C). The sonic muscles are therefore classified as extrinsic drumming muscles. Pale pink in fresh specimens, the muscles became white or yellowish in fixed specimens.

Sexual dimorphism was apparent in the combined weight of the sonic muscles, being 134–240 mg (97.6–106.7 mm SL, N = 5) in males and 60–96 mg (99.5–110.7 mm SL, N = 5) in females (Table 1). The SMSI of males

(mean \pm S.D. = 0.727 ± 0.110) was approximately three times greater than that of females (mean \pm S.D. = 0.244 ± 0.015 , $t = 9.713$, d.f. = 8, $P < 0.001$).

Sound production was accompanied by vibrations of the body wall overlying the swimbladder. However, fin or head movements associated with sound production were not observed. The swimbladder in silver sweeper characteristically included two chambers, interconnected via a small hole (Figure 2A, B), with the tunica externa of the anterior chamber being in contact with the basapophyses of the fourth, fifth and sixth vertebrae, and third rib. The oval posterior chamber had no apparent connection to skeletal elements (vertebrae and ribs).

The sonic muscle was innervated only by occipital nerve branches (Figure 3). The occipital nerve (oc) emerged from the caudal medulla between the vagus (X) and spinal nerves (sp1 and sp2), and passed through the exoccipital foramen, before splitting into dorsal and ventral fascicles. Only two small branches of the ventral fascicles innervated the sonic muscle (Figure 3B), none of the first and second spinal nerves branches doing so.

DISCUSSION

This report is the first to describe the sound characteristics and sound producing system in silver sweeper, the sound resulting from swimbladder

vibrations aided by contractions of a pair of cylindrical sonic muscles. The main frequency of the sound was 100–300 Hz, with a mean duration of about 56 msec. The frequency distribution of the sound (Figure 1C) revealed three harmonically-related peaks, a possible fundamental peak at 100 Hz and two harmonics at 200 Hz and 300 Hz, respectively. However, because the analyzed sounds had been recorded in air in the present study, spectral analysis of sounds recorded under water in aquaria should provide a more exact picture. The sonic muscles, extrinsic owing to their attachments at either end to the pterotic bone and anterodorsal face of the anterior chamber of the swimbladder, respectively (Tavolga, 1971), were innervated by only two branches of the occipital nerve.

Both the sound emitted and the external morphology of the sound producing system in silver sweeper resembled those of the tigerfish, *Terapon jarbua* (Forsskål). The latter, also a Perciform has the similar cylindrical sonic muscles, but produces two types of sound, a frequently emitted short, pulsating sound of about 10 msec duration (used in intraspecific communication) and a longer sound (about 50 msec), accompanying threats (Schneider, 1964). The sound of silver sweeper was similar to the threatening sound of the tigerfish, although short drumming sound was not observed in the present study. The emission of sounds accompanying

agonistic behaviour, observed as the authors approached a school of silver sweeper under water, suggested that such sounds possibly function as a threat to intruders (usually other fish), as in tigerfish.

Silver sweeper are characterized by significant sexual dimorphism of the sonic muscle 3 times larger in males than females, although no external sexually dimorphic features were apparent. In batrachoidid fishes (midshipman), males have larger sonic muscles than females, and the male only produces a long 'hum' call so as to attract females for mating (Fine, 1997). The present findings suggest that male silver sweeper have a greater ability for sound production, which possibly also functioning for sexual recognition during mating. However, this suggestion needs to be confirmed by observation of mating behaviour and examination for seasonal changes in muscle volume.

It is interesting to note, that although the sonic systems of tigerfish and silver sweeper are relatively similar (as discussed above) the innervation patterns of the sonic muscles are quite different, tigerfish use the spinal nerve-sonic muscle system (Schneider, 1964), indicating that the sonic system in the various sound-producing fish species may have evolved independently. However, because the terminology of the occipital nerve has had a controversial history (Parenti & Song, 1996), the innervation pattern in

teraponids should be reexamined using the same occipital nerve definition as used here.

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Figure 1. Example of sounds emitted by silver sweeper. (A):

Representative sonograms (filter bandwidth: 30 Hz) and their oscillograms.

(B): Sonogram (filter bandwidth: 30 Hz) and oscillogram of the waveform of a selected sound (indicated by asterisk in Figure A). (C): Frequency distribution of the sound (pulses) in Figure (B).

Figure 2. Sound producing system (sonic muscle and swimbladder) in silver sweeper. (A): Lateral view of a dissected silver sweeper (female, 108.3 mm SL), showing the sonic muscle (sm) and swimbladder (scale, 1 m). Diagrammatic illustration showing positional relationships of the skull, sonic muscle and swimbladder; lateral (B) and dorsal views (C)(scale, 5 mm). a: anterior chamber, c: cranium p: posterior chamber, pto: pterotic bone, sm: sonic muscle.

Figure 3. Dorsal view (A) of the brain and associated occipital nerve in silver sweeper. Diagrammatic illustration (B) of dissection (A), showing the innervation pattern of the occipital nerve (four). Stars indicate points at which occipital nerve branches (two only) of the ventral fascicles enter the muscle. Dorsal fascicle was not shown here. Dashed line indicates posterior extent of cranium. cc: crista cerebellaris, ce: cerebellum, oc: occipital nerve, pln: posterior lateral line nerve, sm: sonic muscle, sp: spinal nerve, tel: telencephalon, to: tectum opticum, X: vagus nerve, (scale, 1mm).

Table 1. *Sonic muscle size and its SMSI (Sonic Muscle-Somatic Index) in male and female silver sweeper. SMSI was calculated as (total sonic muscle mass/total body mass) X100.*

Specimen	1	2	3	4	5	6	7	8	9	10
Standard Length (mm)	97.6	102.7	103.4	104.5	106.7	99.5	100.1	104.8	108.5	110.7
Body Mass (g)	22.0	31.1	29.4	28.7	28.3	30.0	27.6	29.4	30.3	38.7
Sonic Muscle Mass (g)	0.134	0.190	0.240	0.240	0.216	0.076	0.060	0.074	0.076	0.096
SMSI	0.609	0.611	0.816	0.836	0.763	0.253	0.217	0.252	0.251	0.248
Sex	Male	Male	Male	Male	Male	Female	Female	Female	Female	Female

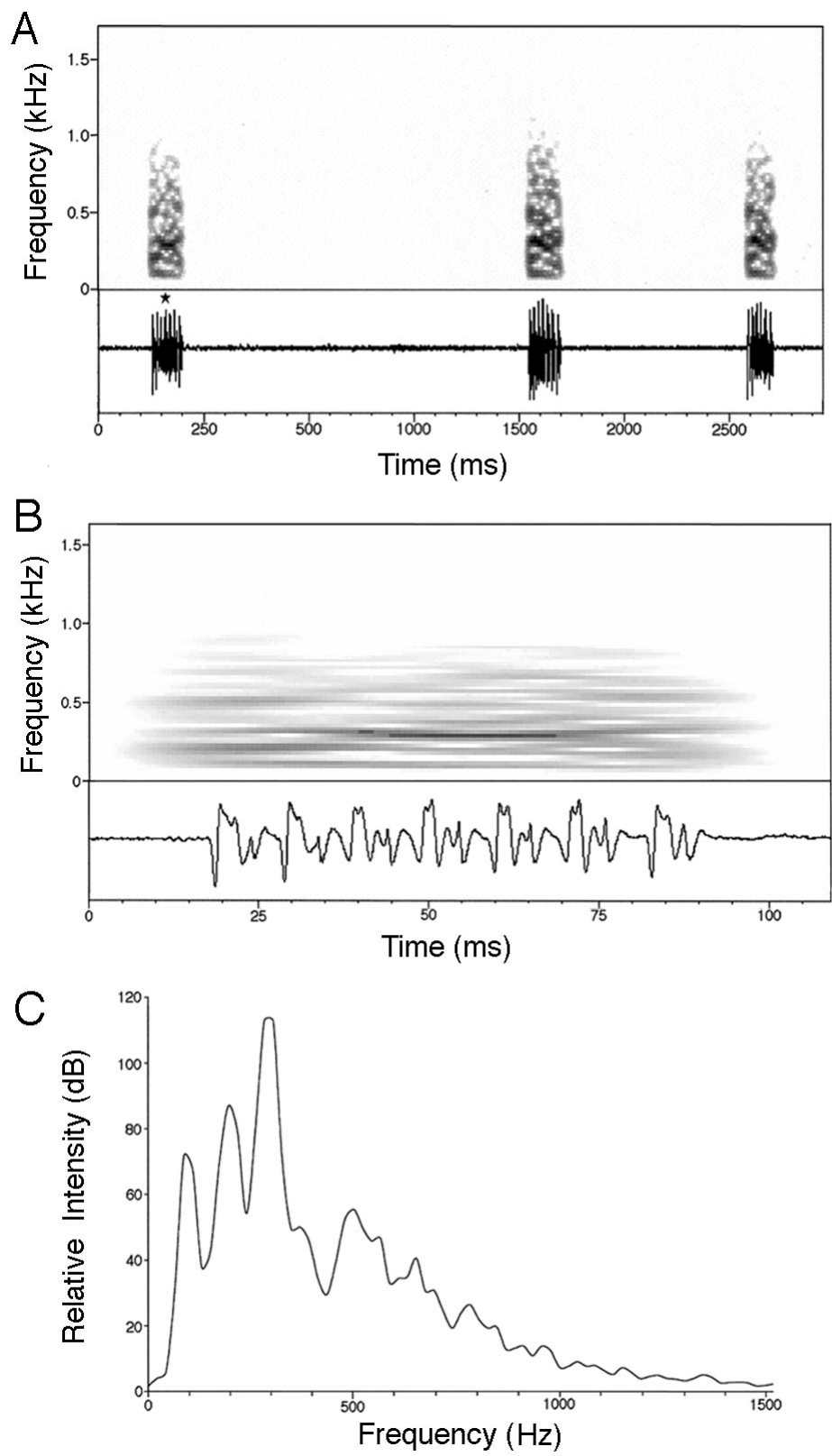


Fig. 1.

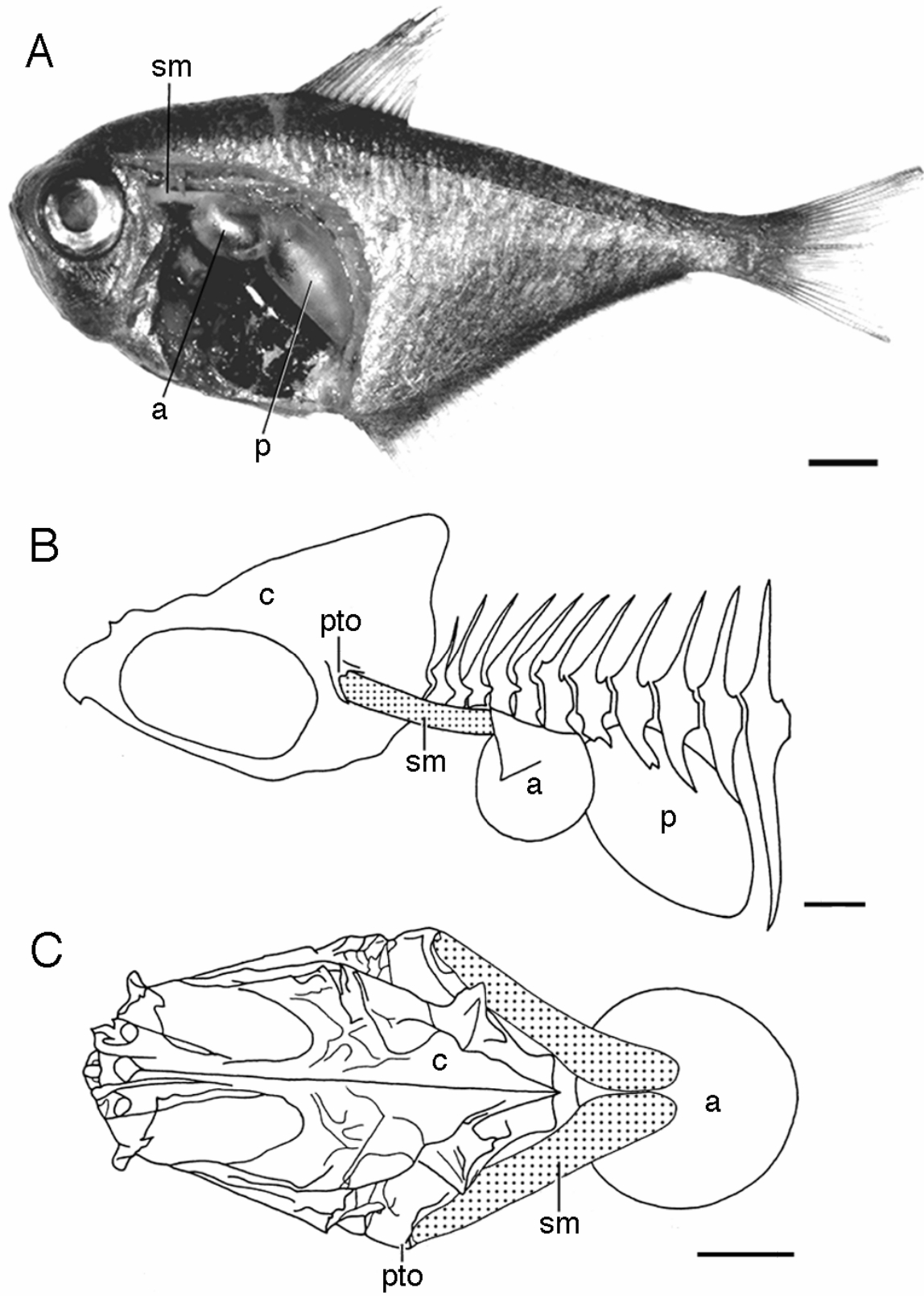


Fig. 2.

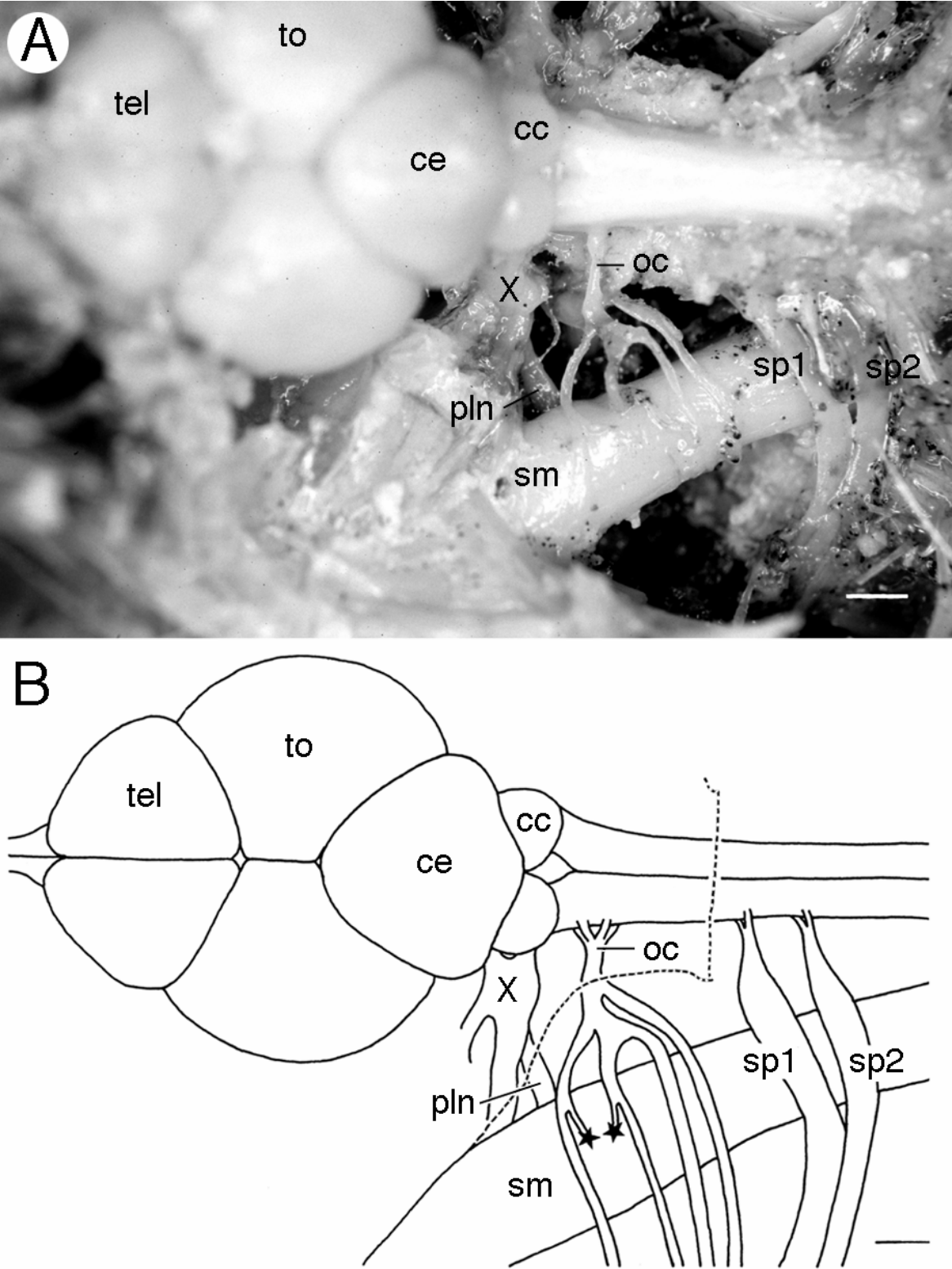


Fig. 3.